OBSERVATIONS ON THE SHELL STRUCTURE OF TRIASSIC AMMONOIDS

by E. T. TOZER

ABSTRACT. Despite mineralogical alteration Triassic ammonoids provide significant data on the layers forming the shell wall and umbilical plug. Two layers (outer and inner test) are recognized in the outer wall. Outer test incorporates growth lines, ornament and colour markings, defines the fundamental architecture, was evidently secreted only on the flanks and venter, probably only at the mantle edge. Inner test deposits are secondary, modifying in various ways the chamber interior, and were secreted both dorsally and ventrally, probably at the mantle surface. *Discotropites* has a dorsal secondary layer within the phragmocone described as dorsal shield and interpreted as a manifestation of the inner test. *Nathorstites*, in contrast, has no dorsal deposit in this position. Secondary deposits secreted within the flanks and venter (preseptal layer of Guex) occur in both phragmocone and in part, but not all, of the body chamber of many Triassic ammonoids. The position of this layer may have exercised buoyancy control. In Ceratitida wrinkle-layer (Runzelschicht) with fingerprint pattern was deposited only on the dorsum and above the umbilical plug and is thus comparable with the *Nautilus* black layer in position, although different in composition and texture. Like the outer test it was probably a secretion of the mantle edge. This kind of wrinkle-layer evidently characterizes Ceratitida and Palaeozoic Ammonoidea but not Phylloceratida, Lytoceratida and Ammonitida. Internal moulds of the flanks of *Nathorstites* have markings (ritzstreifen) with a pattern unlike that of the wrinkle-layer. Accordingly, with Mojsisovics, they are interpreted as impressions of the inner surface of the shell wall, not of wrinkle-layer. *Maclearnoceras enode* sp. nov. is described.

OBSERVATIONS made in the course of a survey of the Triassic Ammonoidea (Tozer 1971*a*) provide new information on some of the less well-known features of the ammonoid shell. This work raises problems of terminology and interpretation and has yielded data which may have phylogenetic significance.

Study of the shell structure of Triassic ammonoids is hampered by the mineralogical alteration that has affected most of the material known from North America and the classical localities of Europe and Asia. Most of the features to be described are relatively gross, and amenable to study under reflected light with a binocular microscope. A few thin sections were examined but as a result of mineralogical alteration they proved unrewarding.

The features considered in this paper are: 1. The outer test. 2. Secondary deposits, consisting of the Preseptal layer, Dorsal shield, and Umbilical deposits. 3. Wrinkle-layer (Runzelschicht) and Ritzstreifen. The structure of the septa and siphuncle are not considered.

OUTER TEST

Following Casey (1961, p. 178) the term 'outer layer of test' (abbreviated here to 'outer test') is applied to the layer of the shell wall which preserves the growth lines and ornament and defines the fundamental architecture of the shell. An example of *Owenites koeneni* Hyatt and Smith (Pl. 126, fig. 3) shows colour markings in this layer. The presence in the outer test of these three features—growth lines, ornament and colour bands—leaves little doubt that the outer test of ammonoids corresponds to the porcellanous ostracum of *Nautilus*, a secretion of the apertural edge of the mantle (Stenzel, *in* Moore 1964, p. K77). This layer is also known as the outer prismatic layer (Erben

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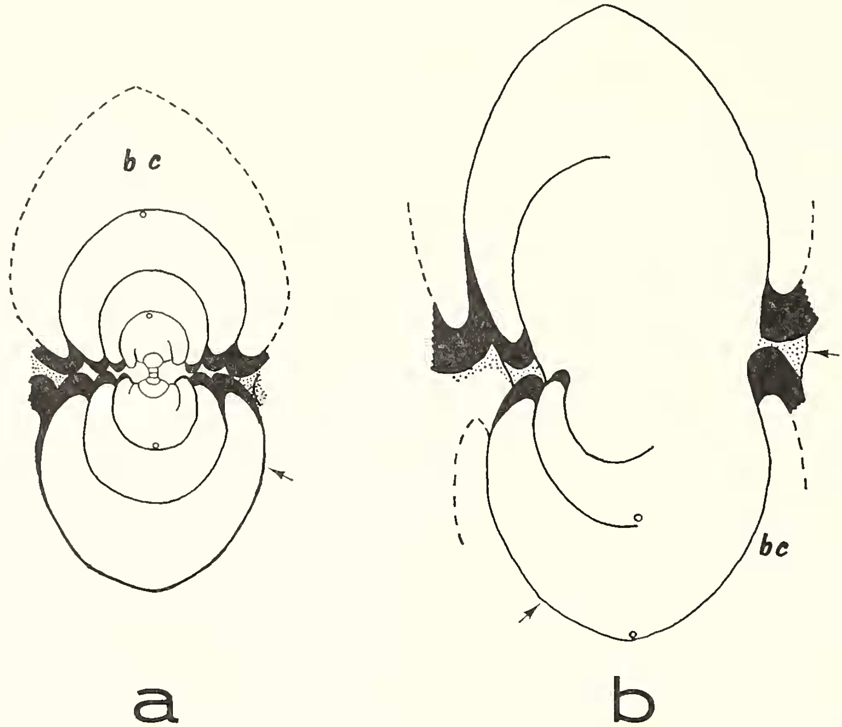
et al. 1968); spherulitic prismatic layer (Mutvei 1964, p. 241) and outer porcelanous [*sic*] layer (Flower 1964, p. 9). Casey (1961) and Birkelund and Hansen (1968, p. 75) have shown that in some Cretaceous ammonoids (*Roloboceras* and *Saghalinites*) the outer test wedges out against the flank or venter of the preceding whorl, and was not secreted on the dorsum.



TEXT-FIG. 1. *Nathorstites macconnelli* (Whiteaves). Camera lucida drawings (×3) of polished sections. (*a*) GSC No. 28027 (GSC loc. 42333). (*b*) GSC No. 28028 (GSC loc. 68264). Liard Formation, Liard River, $3\frac{1}{2}$ miles west of Hell Gate, British Columbia. Solid black indicates thickness of test. Interrupted line is whorl outline defined by internal mould. *bc*, body chamber. Stipple pattern, umbilical deposit. Arrows indicate surfaces on which wrinkle-layer is preserved. Lines traversing umbilical deposit are interpreted as sectional view of wrinkle-layer. Test and umbilical deposits clearly differentiated in (*a*), less so in (*b*).

Sections of shell walls of Triassic ammonoids, with rare exceptions, do not show discrete layers. Nevertheless, as mentioned below, there is clear evidence that the structure was composite. The surface with ornament and growth lines is referred to as outer test although its thickness, in relation to that of the whole shell wall, cannot generally be determined.

Specimens of *Nathorstites macconnelli* (Whiteaves) show the shell wall to be much thicker in the umbilical area than on the flanks and venter (text-fig. 1) and also that the septa are attached to the wrinkle-layer of the preceding whorl (Pl. 124, fig. 2), indicating that within the phragmocone no layer continuous with the outer shell wall secreted on the dorsum. Other specimens (Pl. 124, fig. 4; Pl. 125, figs. 3, 4) show a comparable situation within the body chamber, with the outer wall of the body chamber in the umbilical area wedging out against the wrinkle-layer covering the outer test of the penultimate whorl (text-fig. 3*b*). Whether or not the wedge near the umbilicus includes a layer of outer test has not been determined. Despite the nature of the *Nathorstites* shell wall one should not conclude, with Palframan (1967, p. 1130), that planispiral ammonoids in general did not secrete a dorsal wall. The dorsal shield layer, described below, and interpreted as a manifestation of the inner test, refutes this generalization.

SECONDARY DEPOSITS

Triassic ammonoids show deposits with surface textures unlike that of the outer test and which are secondary in that they appear to be moulded to structures already defined by the outer test. From comparison with *Nautilus* and well preserved Jurassic and Cretaceous ammonites this is to be expected, for in *Nautilus* the porcellanous ostracum is lined by two secondary layers: the nacreous and inner prismatic layers (Mutvei 1964, Erben *et al.* 1968), these, unlike the porcellanous ostracum, being secreted at the surface of the mantle. Mineralogical alteration obscures comparable layers in Triassic ammonoids in which the shell wall is mineralogically and texturally uniform in section, presumably due to recrystallization. *Cladiscites tornatus* (Bronn), according to Mojsisovics (1873, p. 73) provides an exception, showing two layers: the outer with sculpture, the inner being smooth, transparent, and nacreous. Other observations, described below, indicate that at least two layers form the outer wall. For the inner, the name 'inner layer of test' (abbreviated here to 'inner test') may be used (Casey 1961, p. 178). Casey used the term, not only for the portion lining the flanks and venter, but also for the material secreted on the dorsum. In *Nautilus* the most substantial layer inside the porcellanous ostracum is the nacreous layer, and the inner test presumably corresponds with this.

Nathorstites macconnelli shows that the texture of the inner and outer surfaces of the shell wall are different, and suggests that the inner is lined with a secondary deposit. The outer surface (i.e. surface of the outer test) shows the characteristic growth lines (e.g. Pl. 125, fig. 4). The inner surface is reflected by internal moulds which may be more or less smooth (Pl. 125, figs. 1, 2) or pitted with the ritzstreifen (Pl. 125, fig. 4) discussed below.

The actual inner surface of the shell wall has been observed only near the umbilicus. Two specimens, GSC Nos. 28016 (Pl. 125, figs. 3, 4) and 28231 (Pl. 124, figs. 3, 4) show this surface particularly clearly. Both have a band of smooth shell material restricted to the innermost part of the flank, overlying the wrinkle-layer on the underlying whorl. Towards the axis of the umbilicus this smooth material merges with the mass of crystalline calcite sealing the umbilicus (Pl. 125, fig. 4E). The smooth material is clearly the inner surface of the shell wall of the body chamber, wedging out against the underlying whorl, a relationship shown diagrammatically by text-figure 3*b*. The first specimen, a complete phragmocone with most of the body chamber broken off, shows the relationship within the body chamber. The second specimen, which is nearly complete, shows the original limit of the smooth wedge. Interpretation of no. 28231 is facilitated by reference to No. 28232, which although presumably not fully grown, is nevertheless complete because it preserves the peristome with a notched rostrum (Pl. 124, figs. 5, 6). The length of the body chamber is $1\frac{1}{8}$ whorls. The smooth layer and length of the body chamber, although not shown by the illustrations, were observed by breaking the specimen. The extent of the smooth band on the inner flank corresponds with that of the rostrate peristome, confirming that the limit of the smooth band shown by no. 28231 (Pl. 124, fig. 4) indicates the terminal point of attachment of the body whorl. These specimens thus show the surface of both the outer and the inner test. The outer, with growth lines, compares with that of the *Nautilus* porcellanous layer, and the smooth inner surface is like the inside of the nacreous layer.

Triassic ammonoids also show secondary material in three situations: (i) on the flanks and venter, where they form the preseptal layer (Guex 1970); (ii) on the dorsum, as a layer obliterating or modifying the ornament of the outer test of the preceding whorl, the 'dorsal shield' of Casey (1962, p. 264); (iii) in the umbilicus, where they form a callus, or plug.

Preseptal layer. On the flanks and venter differentiation of inner and outer test is based partly on direct observation, but mainly on the differences shown by comparing the ornament of internal moulds with that of the outer test. A direct observation is provided by *Maclearnoceras enode* n. sp. (Pl. 128, figs. 3, 4), described in the appendix. The only specimen is so preserved as to leave little doubt that the shell wall, at least on the initial part of the body chamber, is composed of these two layers. The outer test, attaining a maximum thickness of 0·2 mm is corrugated to form ribs on both the inner and outer surface (Pl. 128, fig. 3). The inner test (maximum thickness 0·5 mm) has a corrugated outer surface, moulded to that of the outer test, but the inner surface, lining the body chamber, and the surface to which the septa were attached, is smooth.

This specimen provides grounds for interpreting many Triassic ammonoids in which the ornament and whorl section, as preserved on an internal mould, differs conspicuously from that shown by the outer surface. These discrepancies are shown in *Frankites sutherlandi* (McLearn) (Pl. 128, figs. 5–9) in which the periphery, where the

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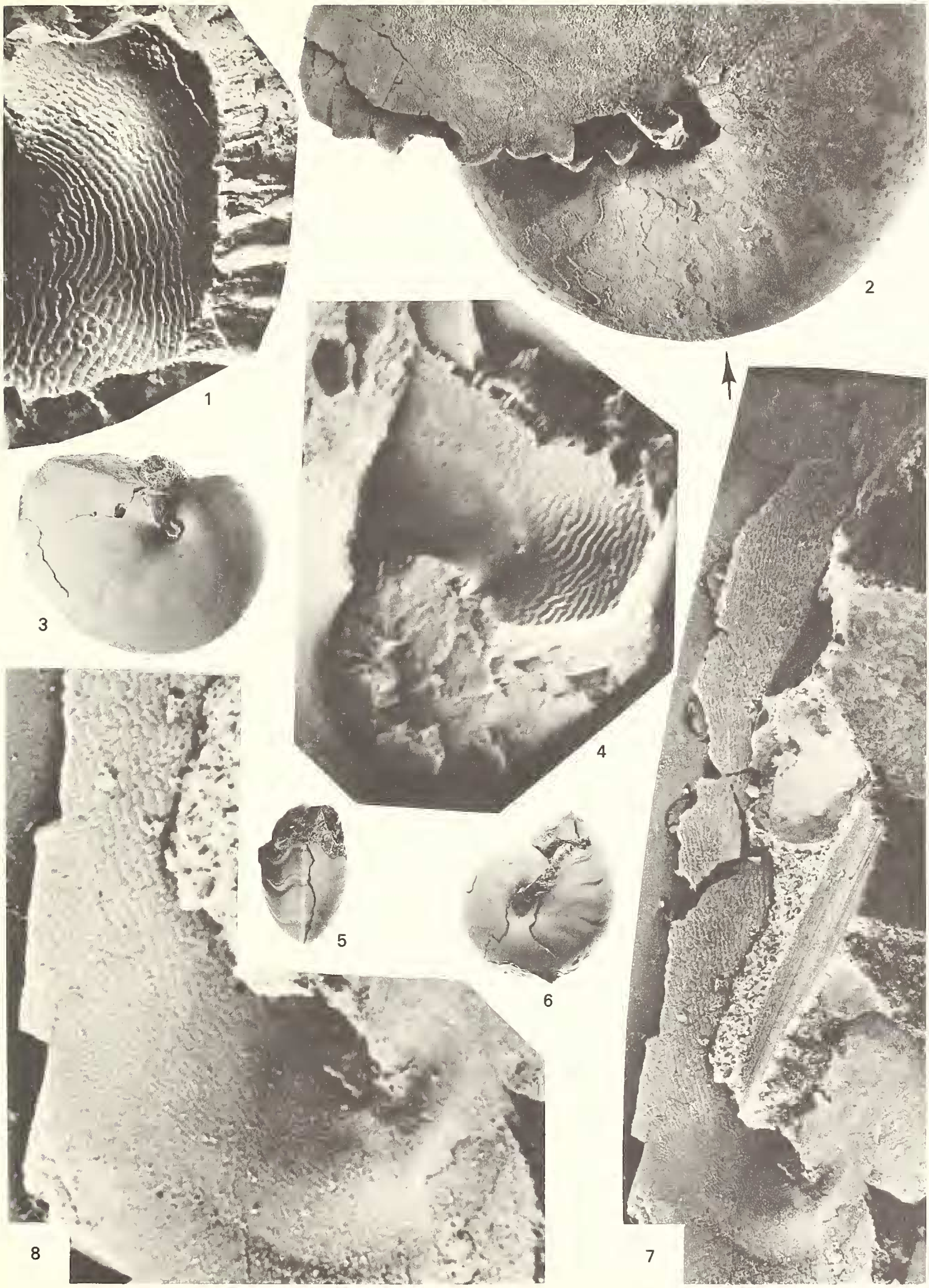
EXPLANATION OF PLATE 124

Specimens coated with ammonium chloride.

Figs. 1–7. *Nathorstites macconnelli* (Whiteaves). 1, (×16), GSC No. 28028, Liard Formation, 323 feet below Triassic-Cretaceous contact, Liard River, $3\frac{1}{2}$ miles west of Hell Gate, British Columbia (GSC loc. 68264), Upper Ladinian, Sutherlandi Zone, wrinkle-layer in umbilical area of sectioned specimen (text-fig. 1*b*). 2, (×4), GSC No. 28026, Liard Formation, 280 feet below Triassic-Cretaceous contact, Liard River, $3\frac{1}{2}$ miles west of Hell Gate, British Columbia (GSC loc. 42335), Upper Ladinian, Sutherlandi Zone, lateral view of portion of incomplete phragmocone with remnants of last eight septa visibly attached to the wrinkle-layer of the preceding whorl, arrow indicates position of last septum. 3, 4, GSC No. 28231, horizon and locality as fig. 1 (GSC loc. 68264), 3 (×1) lateral view of whole specimen, mostly preserved as internal mould except in umbilical area, body chamber length 1 whorl, 4 (×16) oriented as 3, shows detail of umbilical area, described in text. 5, 6 (×1), GSC No. 28232, Liard Formation, 310 feet below Triassic-Cretaceous contact, Liard River, $3\frac{1}{2}$ miles west of Hell Gate, British Columbia (GSC loc. 42334), Upper Ladinian, Sutherlandi Zone, ventral view (5) shows notched rostrum, lateral view (6) the side of the peristome, body chamber length $1\frac{1}{8}$ whorls. 7 (×8), 8 (×16), GSC No. 28230, Liard Formation, about 40 feet below Triassic-Cretaceous contact, Liard River, $2\frac{1}{2}$ miles west of Hell Gate, British Columbia (GSC loc. 42351), Upper Ladinian, Sutherlandi Zone. 7 illustrates lateral view of final portion of phragmocone, from umbilicus to venter (7, top), wrinkle-layer cover sentire dorsum, on greater part ridges are radial but at umbilicus they sweep into a spiral (8).



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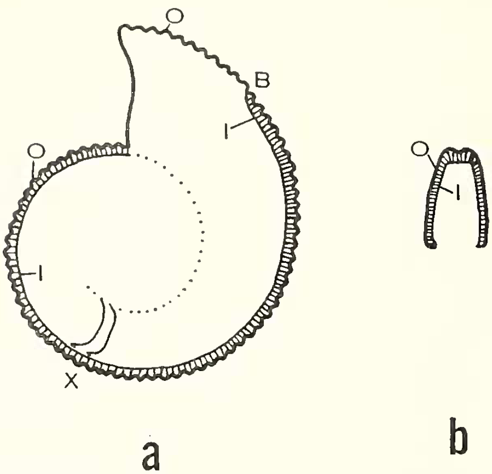
outer test is preserved, has rounded ventral shoulders, abrupt rib terminations at the shoulder, and a sulcus on the siphonal line (Pl. 128, fig. 8). The mould, in contrast, on both the phragmocone and the initial part of the body chamber (Pl. 128, figs. 6, 9) has well defined ventral shoulders and an almost smooth venter, with no trace of a sulcus. Near the aperture, however, there is an abrupt change to a condition where the ornament of the mould and the outer test nearly correspond (Pl. 128, figs. 6, 9). Obviously the inside and outside of the *Frankites sutherlandi* shell wall were very different, except near the aperture. The interpretation of this discrepancy (text-fig. 2) follows that provided by Guex (1970) to account for features shown by internal moulds of Jurassic Dactylioceratidae, in which the initial part of the body chamber has a zone of smooth ornament followed abruptly by a zone of sharp ornament (Guex 1970, p. 2, Pl. 2, fig. 3). Guex named the material responsible for suppressing the ornament in the smooth zone as the preseptal layer. In his interpretation the preseptal layer and 'conotheca' (i.e. outer test) are only partly in contact with a hollow space occupying the summits of ribs and spines. *Maclearnoceras enode* gives no indication that a hollow space existed, on the contrary, the preseptal layer was apparently firmly cemented to the outer test with the outer surface of the preseptal layer faithfully reproducing the rib pattern of the inner surface of the outer test (Pl. 128, fig. 3).

The lateral ribs of *Frankites sutherlandi* are more sharply defined on the test than the mould, indicating that the preseptal layer was deposited on the flanks as well as the venter. A development of preseptal layer on the flank is clearly shown by *Muensterites glaciensis* (McLearn), the ribs on the outer test bearing tubercles which are obliterated on the internal mould (Pl. 127, fig. 6).

The function of the preseptal layer is unknown. It may have been merely a layer to strengthen and make smooth the inside of the body chamber. But if this alone was its function, why was it not secreted throughout the whole length of the body chamber? Or it may have served some role in muscle attachment, like the annular ridges and elevations known at the posterior end of the body chamber of some nautiloids (Teichert, *in* Moore 1964, p. K 27) and ammonoids (Jordan 1968). There is also the possibility that it may have contributed to bouyancy control. Being fairly thick, its mass, in relation to the mass of the whole animal, must have been appreciable. The fact that it terminates abruptly, instead of merely tapering off, suggests that its limit in the body chamber, may have been rigidly defined, and that its extent may be related to the regime of the animal. In other words the preseptal layer of the body chamber may have represented a layer of ballast, precisely positioned in relation to the adult aperture, and thus exercising a degree of control over the position of the animal in life.

Dorsal shield. The term 'dorsal shield' was introduced by Casey (1962, p. 264) for the thick layer of shell secreted on the dorsum of *Douvilleiceras*, serving to render smooth what would otherwise be a very rough roof for the successive body chambers, rough because the venter of *Douvilleiceras*, from an early stage, bears strong tubercles. *Douvilleiceras* from the Queen Charlotte Islands show this feature well (McLearn 1972). One specimen (GSC No. 5014 d) shows that the dorsal shield is not merely a layer secreted in the adult body chamber, but extends back behind the last septum. This specimen also shows lamination of the test, and it appears that the dorsal shield represents a part of the inner test.

The Triassic ammonoid *Discotropites* has a structure comparable in position but with spiral sculpture. The presence of this layer on *Discotropites* was noted by both Suess (1870, p. 315) and Mojsisovics (1893, pp. 283, 287). Suess considered it a form of wrinkle-layer (runzelschicht); Mojsisovics regarded it as a form of 'Epidermiden', but did not employ the name runzelschicht. The thickness varies considerably. Mojsisovics' illustrations (1893, Pl. 130, fig. 13; Pl. 131, figs. 1, 4, 10) show thin developments of the layer. Of the specimens he studied, a thick development is shown by the original of his Plate 130, fig. 12, for which he illustrated only the suture line. I have seen this specimen at the Geologische Bundesanstalt, Vienna. A published illustration of the thick development of this layer has been provided by Smith (1927, pl. 11, fig. 8) for *Discotropites laurae* (Mojsisovics). A plaster cast of Smith's specimen shows the layer to be about 1 mm thick at the venter. Another specimen from British Columbia (Pl. 128, figs. 1, 2) shows a mere film, 0·1 mm thick or less. As noted by Suess (1870, p. 315) this spirally sculptured layer has a close counterpart in Jurassic *Amaltheus*. Most writers who have discussed the *Amaltheus* layer (e.g. Suess 1870, Zittel 1895, p. 407, fig. 1112; Walliser 1970, pl. 4, fig. 5) have considered it to be wrinkle-layer (runzelschicht). The properties of true wrinkle-layer are discussed below. Two differences distinguish the spirally sculptured layer of *Discotropites* and *Amaltheus* from wrinkle-layer. First, the *Discotropites* layer has a wholly spiral sculpture, unlike the dominantly radial, fingerprint pattern of true wrinkle-layer; second, this layer is of variable thickness, and when thick, much thicker than wrinkle-

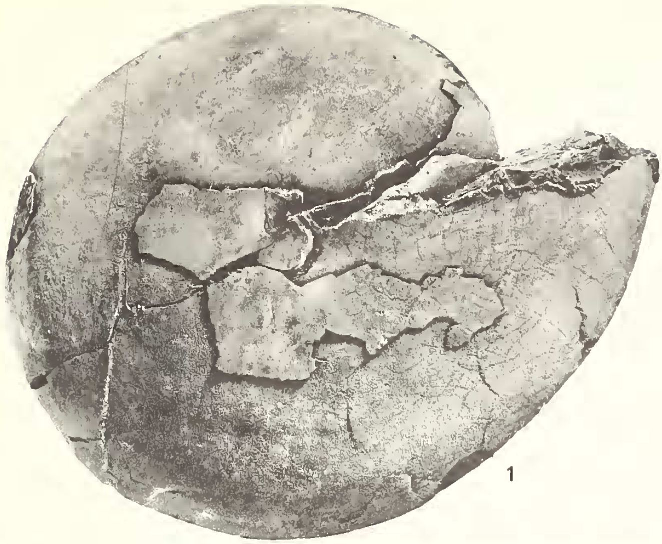


TEXT-FIG. 2. Diagrammatic median section (*a*) and whorl section of phragmocone (*b*) of *Frankites sutherlandi* (McLearn) based on GSC Nos. 18903 and 28025 (Pl. 128, figs. 5–9). O (heavy line) represents the outer test, I (ruled), the preseptal layer, B the place where the preseptal layer ends as indicated on the internal mould by the change from the zone of smooth ornament to zone of sharp ornament. X marks position of last septum. Thicknesses of layers schematic.

EXPLANATION OF PLATE 125

Specimens coated with ammonium chloride. Arrow marks position of last septum.

Figs. 1–4. *Nathorstites macconnelli* (Whiteaves). Lateral views. 1 (×1), 2 (×4), GSC No. 28014, GSC loc. 42351 (see explanation, Plate 124). Body chamber >1 whorl, probably complete and adult. 2 shows detail of umbilical area with wrinkle-layer covering outer test and extending about ¼ whorl beyond aperture. 3 (×1), 4 (×20), GSC No. 28016, GSC loc. 42335 (see explanation, Pl. 124). 4 shows detail of inner flank and umbilical area with ritzstreifen pits on internal mould of body chamber (A), surface of outer test with growth lines (B), overlain by wrinkle-layer (C). Near umbilicus wrinkle-layer is overlain by wedge of smooth shell (D), the inner margin of the shell wall of the body chamber. (E) is broken face of body chamber shell wall where parallel to axis of coiling. Boundary between shell wall and umbilical plug not discernible owing to recrystallization. Small granules on (D) are of ammonium chloride. Ritzstreifen certainly present only on body chamber.



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layer, which invariably seems to be a single lamina. 'Dorsal shield' seems a more appropriate term for the *Discotropites* layer. Because the *Discotropites* dorsal shield may be thick, thin, or absent it may be interpreted as a secretion of the mantle surface, not of the mantle edge. If so it was probable originally nacreous and a structure of the inner test, comparable with the preseptal layer, but dorsal instead of ventral in position.

Umbilical deposits. A number of Triassic ammonoids have the umbilicus sealed by a callus or plug, as does *Nautilus pompilius* Linné. The *Nautilus* callus is a milk-white porcellanous substance (Gregoire 1962, p. 9), different in appearance from the nacreous material forming the thick inner layer of the shell wall. Examples of *Nathorstites macconnelli* preserving shell in the umbilical area have much in common with *Nautilus pompilius* but owing to mineralogical alteration exact homologies cannot be established. In section, material of one texture forms the shell wall, of another the callus, and in places the boundary between the two is clearly defined (text-fig. 1). Polished and thin sections have failed to resolve the structure of the shell wall. Part is outer test but some, or all, where it is thickest in the umbilical area may have been secondary nacreous material. The position and overall appearance of the callus deposit invites comparison with that of *Nautilus*.

The helicolateral deposits (Nassichuk 1967) described on the Carboniferous goniatite *Clistoceras globosum* Nassichuk may also be comparable. Adult *Clistoceras* is imperforate, like *Nautilus pompilius* and *Nathorstites* (e.g. Nassichuk 1967, pl. 28, fig. 10). Sections made by Nassichuk show that *Clistoceras*, in terms of the architecture of the shell wall, has an unusually undercut umbilicus (Nassichuk 1967, text-figs. 1, 2). Although I am unaware of any ammonoid showing comparable undercutting there are other ammonoids with distinctly undercut umbilical walls, e.g. *Tropites subquadratus* Silberling (Silberling 1959, pl. 3, fig. 5). In *Clistoceras* deposits fill most of the umbilical cavity, including the undercut portion. This material, named the 'helicolateral deposit' by Nassichuk, extends well towards the middle of the flank. Specimens from which the outer whorl has been stripped (e.g. Nassichuk 1967, pl. 28, figs. 2, 6) present a unique appearance, particularly as the deposits bear what seem to be growth lines. These features led Nassichuk to conclude that the helicolateral deposits are primary (i.e. secreted in front of the aperture, before secretion of the next whorl), and are not homologous with the umbilical callus of *Nautilus*. On the other hand the helicolateral deposits may be homologous with the callus of *Nautilus* and *Nathorstites* since:—firstly, secretion in front of the aperture has not been demonstrated (indeed the example of *Clistoceras* with a body chamber (Nassichuk 1967, p. 28, fig. 10) shows no deposit beyond the aperture); secondly, the presence of helicolateral deposits has been demonstrated only between whorls; and thirdly, the growth lines that suggest a primary deposit may be interpreted as impressions from the outer test of the succeeding whorl. Undercut umbilical walls are not unique; this feature of *Clistoceras* is one of degree, not of kind. Therefore the helicolateral deposits of *Clistoceras* are not unique but owe their extraordinary appearance to the unusually undercut nature of the umbilical wall.

WRINKLE-LAYER (RUNZELSCHICHT) AND RITZSTREIFEN

The terms 'Runzelschicht' and 'Ritzstreifen' were introduced by the Sandbergers (1850, pp. 58, 93, 121). The English equivalent term for Runzelschicht is 'wrinkle-layer'

(Foord and Crick 1897, p. xx). For Ritzstreifen (Scratch-grazes) there seems to be no wholly satisfactory English term. Foord and Crick's (1897, p. xx) use of 'Epidermids' invites confusion because Barrande (1877) coined the term 'Épidermides' to include both Runzelschicht and Ritzstreifen. Clausen (1969, p. 104) treats Ritzstreifen as a synonym of Runzelschicht; House (1971) and Senior (1971) use the term 'ventral wrinkle-layer'. The nomenclature of Clausen, House, and Senior would be satisfactory if it was entirely certain that Ritzstreifen and Runzelschicht are manifestations (the impression and layer respectively) of one and the same thing, as held by Barrande, Clausen, House, Senior, and others. But it will be shown below that Ritzstreifen may not be the impressions of wrinkle-layer. Accordingly for descriptive purposes it seems more appropriate to adopt the more objective terminology employed by the Sandbergers (and also Mojsisovics), which was to use the different names.

Definition of wrinkle-layer (*Runzelschicht*). Runzelschicht had been recognized by Keyserling (1846, pp. 274–275) before the publication of the Sandbergers work. The feature recognized by Keyserling and the Sandbergers is a thin layer superimposed on the outer test of Devonian goniatites. There is no doubt that Keyserling and the Sandbergers were describing a distinct layer which they identified only on the dorsum. To Keyserling (1846, p. 275) it was a deposit laid down 'an der sogenannten Bachseite des Umganges'; to the Sandbergers (1850, p. 58, footnote), a deposit on the 'Rückenoberflache', i.e. a deposit on that part of the outer test of the earlier formed whorl which forms the dorsum of the later chamber.

Since the time of publication of these early papers the names Runzelschicht or wrinkle-layer have been applied to a number of features. Some are certainly closely comparable with the layer named by the Sandbergers, others less certainly so, some certainly not. In order to avoid ambiguity a definition, and reference to a typical example, is essential. Keyserling (1846, p. 275) recognized wrinkle-layer on ammonoids now referred to *Tornoceras*, *Beloceras* and *Ponticeras* (?). In addition to these three the Sandbergers (1850, p. 58) described wrinkle-layer on representatives of what are now known as *Maenioceras*, *Manticoceras*, and *Pharciceras*. For present purposes the layer as developed on *Tornoceras* may be taken as typical and representative. This seems entirely

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EXPLANATION OF PLATE 126

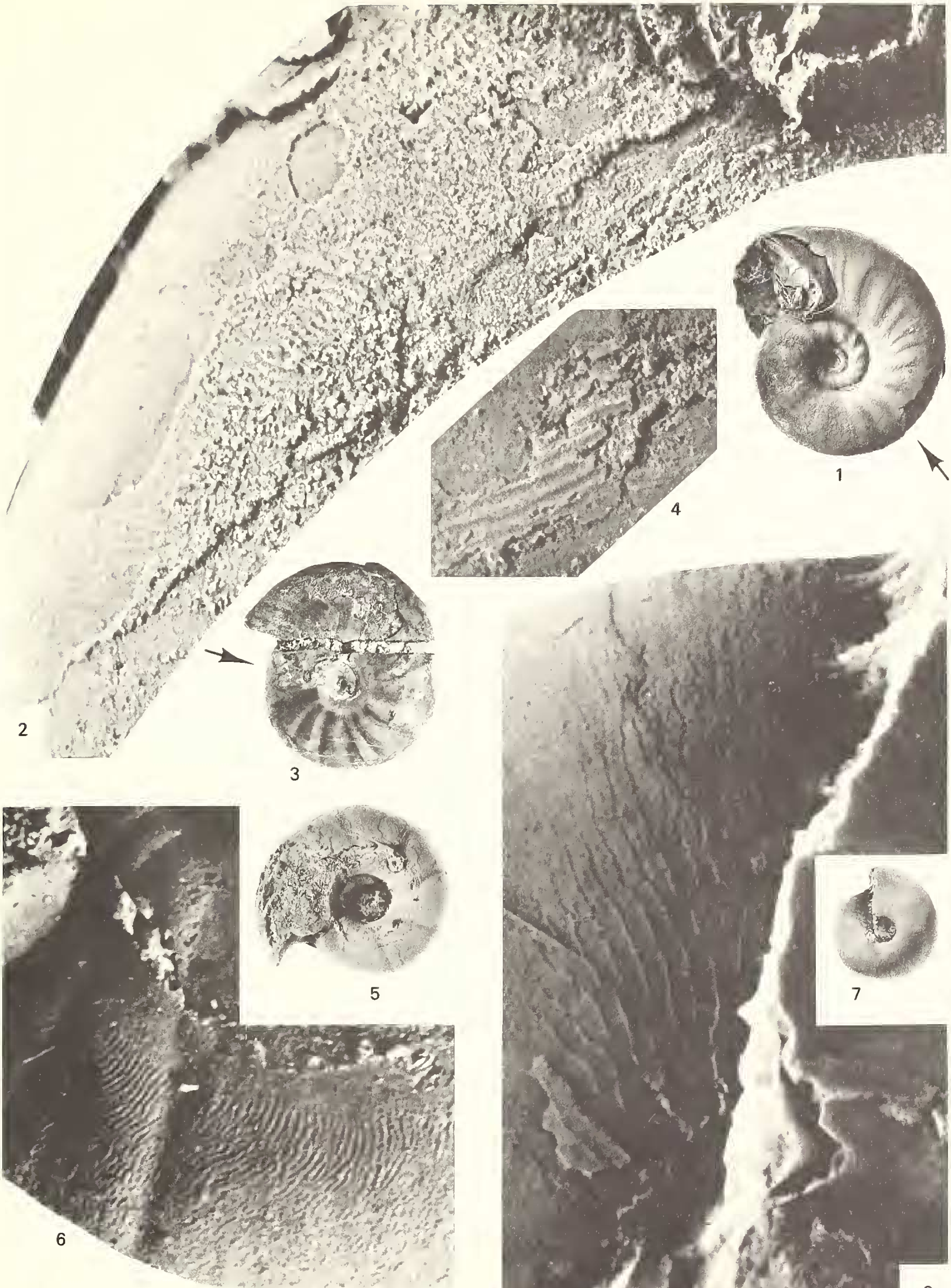
Specimens, except 3, coated with ammonium chloride. Arrows mark position of last septum.

Figs. 1 (×1), 2 (×16). *Nordophiceras spathi* (Kummel and Steele). GSC No. 28018. North side Mill Canyon, about 2 miles north-east of Crittenden Ranch, Elko County, Nevada (GSC loc. 64685). Lower Triassic, Smithian (Silberling and Tozer 1968, p. 29). Most of specimen preserves outer test with wrinkle-layer (fig. 2) superimposed, extending for 8 mm, measured at venter, beyond aperture.

Figs. 3 (×1), 4 (×16). *Owenites koeneni* Hyatt and Smith. GSC No. 28017. Locality as above. Mostly preserved with outer test retaining reddish-brown colour bands (dark in figure 3). Small patches of wrinkle-layer (fig. 4) preserved for $\frac{1}{4}$ volution beyond aperture.

Figs. 5 (×2), 6 (×16). *Juvenites septentrionalis* Smith. GSC No. 28019. Locality as above. Phragmocone with outer test and wrinkle-layer.

Figs. 7 (×1), 8 (×16). *Proarcestes* sp. GSC No. 28020. Bluff 10 miles south-east of Mount Mary Henry, British Columbia (GSC loc. 68284). Lower Ladinian, Poseidon Zone. Complete phragmocone preserving outer test and wrinkle-layer (fig. 8), removed from complete specimen with $1\frac{1}{4}$ whorls of body chamber.



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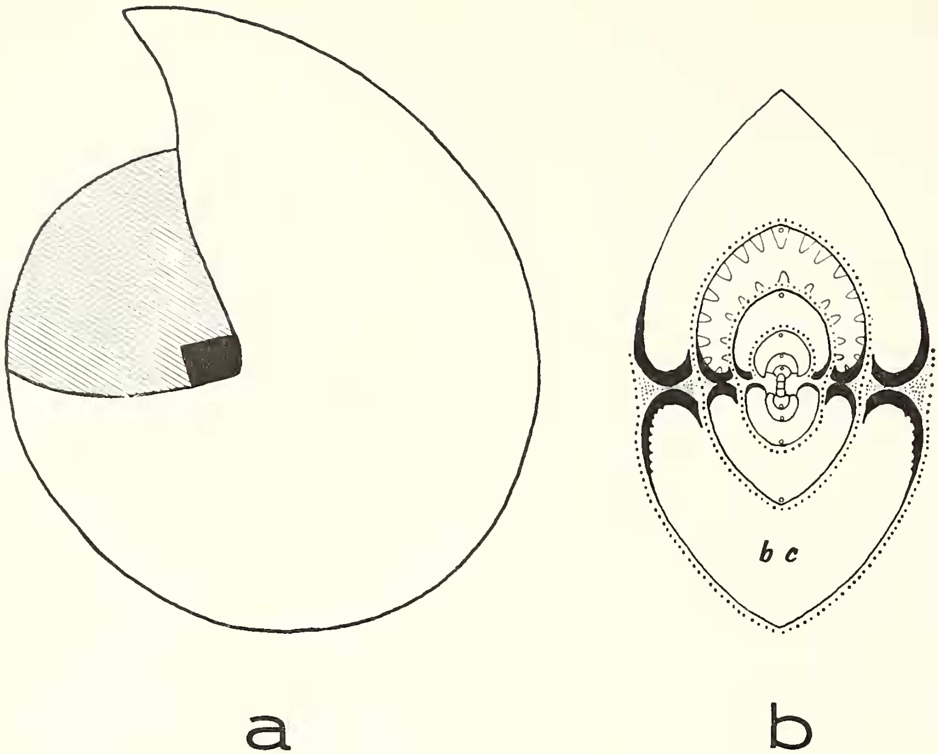
justified: it is a genus on which the layer was studied by Keyserling and the Sandbergers; it is clearly shown on some of the old illustrations (e.g. Sandberger and Sandberger 1850, pl. 10, fig. 14); and excellent photographic illustrations have been provided by House (1965, pl. 6, fig. 42, pl. 8, figs. 71, 72, pl. 9, figs. 78, 79). The features of wrinkle-layer are: it is thin, apparently a single lamina, encrusting the surface of the outer test on the dorsum; it is also characterized by a very distinctive texture of small ridges and furrows, resembling human fingerprints. Walliser (1970) and House (1971) have distinguished several kinds of pattern and suggested that a more refined classification may have systematic significance. Keyserling's comparison with fingerprints nevertheless remains apt to characterize, at least in a gross sense, the most distinctive feature of wrinkle-layer, which has for long been recognized on Triassic and Carboniferous ammonoids in addition to those of Devonian age.

Very different from the layer with fingerprint pattern are a number of features which have been described in the literature as wrinkle-layer. First there is the spirally sculptured layer of *Discotropites* and *Amaltheus*, which does not closely resemble true wrinkle-layer. There is also the granular wrinkle-layer, the 'gröbkornig runzelschicht' of Mojsisovics 1873, p. 69, pl. 24, fig. 2 described on *Sageceras haidingeri* (Hauer). Mojsisovics described this as a form of wrinkle-layer, unlike the typical variety, and as resembling in texture the black layer of *Nautilus*. Examination of the specimen described by Mojsisovics (illustrated here Pl. 127, figs. 4, 5) as preserving this kind of layer, has failed to convince me that it is other than an inorganic crust, deposited on the outer test. Wrinkle-layer as interpreted by Miller (1947, pl. 3), and Teichert (*in* Moore (ed.), 1964, p. K15) is a feature revealed by the etching or weathering of the nacreous layer and is certainly not the same as the thin discrete layer discriminated by the Sandbergers.

On the other hand the dorsal wrinkle-layer identified by Senior (1971) on Jurassic Graphoceratidae appears to be closely comparable, in terms of thickness and position, with true wrinkle-layer. The texture, however, is not the same, the wrinkling being much finer, and the fingerprint pattern absent.

Definition of Ritzstreifen. The Sandbergers (1850, p. 121) introduced the term Ritzstreifen to describe markings preserved on moulds providing an impression of the surface of the inside of the lateral and ventral parts of the ammonoid whorl. In the same work (1850, p. 93) they also use the term 'Einritzung des Manteleindrucks' for this feature. What they were describing is clearly shown by their illustration of '*Goniatites lamed* var. *cordatus*' (1850, pl. 8, fig. 6b) (a representative of *Manticoceras*) on which the internal mould shows more or less radial striae indicating that a patterned surface lined the lateral and ventral parts of the whorl. Photographic illustrations of *Manticoceras ritzstreifen* have been provided by Clausen (1969, pl. 26, figs. 10, 12, 13, 14). The pattern displayed by the ritzstreifen of *Manticoceras* resembles, at least in a gross way, that of wrinkle-layer. In other ammonoids, however, the impressions derived from surface of the lateral and ventral interior take the form of pits instead of ridges, indicating a surface wholly unlike that of wrinkle-layer. Judging from the observations of Walliser (1970, p. 121, text-fig. 5D, pl. 2, figs. 1, 6) this is the case in *Tornoceras* and *Maenioceras*, both of which have wrinkle-layer with fingerprint pattern on the dorsum, and ritzstreifen in the forms of pits on the flank. Ritzstreifen, unlike wrinkle-layer, seem to be known only from impressions and in consequence their interpretation is the more difficult. The



TEXT-FIG. 3. Diagrammatic restored side view (*a*) and section (*b*) of *Nathorstites macconnelli* (Whiteaves) about ×1 but thickness of shell layers and relief of surface responsible for ritzstreifen schematic.

(*a*) based only on GSC No. 28014 (Pl. 125, fig. 1); black area indicates where wrinkle-layer is actually preserved; patterned area its presumed original extent in relation to the aperture.

(*b*) shows distribution of wrinkle layer (dotted line) on outer and inner whorls. Solid black indicates shell wall, with small elevations at posterior end of body chamber forming ritzstreifen (Pl. 125, fig. 4). Stipple pattern indicates umbilical deposit, *bc*, the start of the body chamber. Septa of inner whorls not shown. Wrinkle-layer of outer whorl encrusting umbilical deposit is shown on Plate 124, fig. 1; the layer passing beneath the wedged out portion of the body chamber on Plate 124, fig. 4 and Plate 125, fig. 4. The layer is shown to traverse the umbilical area of inner whorls from interpretation of GSC No. 28028 (text-fig. 1*b*), but the evidence that it does so is not conclusive.

relationship between the two will be discussed after description of wrinkle-layer and ritzstreifen in Triassic ammonoids.

Wrinkle-layer of Triassic Ammonoids. The occurrence of wrinkle-layer closely resembling that of *Tornoceras* is well known in Triassic ammonoids (Mojsisovics 1873–1875). A review of the literature and my own studies have established the presence of wrinkle-layer with fingerprint pattern in the following families of Ceratitida: Ophiceratidae (*Nordophiceras*); Melagathiceratidae (*Juvenites*); Parananannitidae (*Paranannites*, *Owenites*); Aspenitidae (*Aspenites*); Megaphyllitidae (*Megaphyllites*); Gymnitidae (*Placites*);

Ptychitidae (*Ptychites*); Carnitidae (*Carnites*); Pinacoceratidae (*Pompeckjites*); Danubitidae (*Arctohungarites*); Longobarditidae (*Intornites*); Nathorstitidae (*Nathorstites*); Cladiscitidae (*Paracladiscites*); Arcestidae (*Proarcestes*, *Arcestes*); Sphingitidae (*Sphingites*); Joannitidae (*Joannites*); Cyrtopleuritidae (*Drepanites*, *Hauerites*); Lobitidae (*Lobites*); Didymitidae (*Didymites*). Of these I have examined well preserved representatives of all except *Carnites*, *Paracladiscites* and *Sphingites*. In every case the presence of wrinkle-layer has been confirmed, or observed for the first time, on the dorsum. None, with the possible exception of *Megaphyllites* (discussed below) provide any indication that a comparable layer lined the ventral and lateral parts of the chambers. Good preservation is necessary in order to see wrinkle-layer. This limits assessment of its systematic significance in that it is often impossible to decide whether absence is true, or due to unfavourable preservation. Most that show it clearly are smooth forms. None of the really rough-shelled Ceratitida are known to have wrinkle-layer. It is therefore of some significance that *Drepanites* (Pl. 127, figs. 1, 2), a relatively smooth member of a rough-shelled family, shows wrinkle-layer, indicating that the ability to secrete this layer was not lost in all rough-shelled families of Ceratitida.

The wrinkle-layer of the ammonoids listed above has the fingerprint pattern. There is considerable variation in the spacing of the ridges. They are closest in forms like *Juvenites* (Pl. 126, fig. 6) (about 20 ridges to the mm); most widely separated in *Proarcestes* (Pl. 126, fig. 8) (about 4). *Nathorstites* (about 10) falls in between and has a similar pattern to *Tornoceras*. Further work on the lines proposed by Walliser (1970) and House (1971) will perhaps result in a more refined classification.

Nathorstites macconnelli (Whiteaves) shows the pattern and relationships of the wrinkle-layer particularly clearly. It is a layer of calcareous material, about 0·04 mm thick, superimposed on the outer test (Pl. 125, fig. 4). GSC No. 28230 (Pl. 124, figs. 7, 8) shows the arrangement of the ridges to be radial over the greater part of the flank, and sweeping into a spiral in the immediate umbilical area. The details of the pattern in the umbilical area are particularly clearly shown by No. 28028 (Pl. 124, fig. 1). No. 28026 (Pl. 124, fig. 2) shows the layer within the phragmocone, with the septa of the next whorl attached. The layer has also been observed on nuclei 9 mm in diameter. Nos. 28231 and 28016 show the relationships of the wrinkle-layer in the umbilical area, both at the aperture (Pl. 124, figs. 3, 4) and within the body chamber (Pl. 125, figs. 3, 4). On these specimens the wrinkle-layer near the umbilicus is covered by smooth (originally nacreous?) shell material representing the inner test of the wedged out portion of the succeeding volution. Furnish and Glenister (1971) have described a specimen of *Mescalites discoidalis* (Böse) with wrinkle-layer similarly overlain by smooth material. Polished sections of *Nathorstites* (text-fig. 1) show a dark line traversing the umbilical deposit. These are at the same 'level' as the wrinkle-layer and it is suggested that they indicate its position in the umbilical area. No. 28014 (Pl. 125, figs. 1, 2), probably complete and fully grown, shows wrinkle-layer overlying the umbilical plug and on the inner flank, where it extends about one-quarter volution beyond the aperture. On this specimen the layer ends abruptly and the terminal boundary where preserved on the inner flank, is radial. This boundary may indicate the true edge and limit of the layer. If so, and if the radial course was followed to the venter, the complete specimen would have had the appearance indicated by text-figure 3*a*. Many specimens of *Nathorstites*, preserved as internal moulds, show an impression of the inside of the flanks and venter. None shows a trace of the pattern of the wrinkle-layer but some show minute pits which may be described as ritzstreifen.

Ritzstreifen of Triassic Ammonoids. The best known occurrence of ritzstreifen among Triassic ammonoids is that of *Megaphyllites* (Mojsisovics 1873, pp. 45–46). Mojsisovics described them as 'Ritzstreifen des Manteleindruckes', presumably implying that the markings provide an impression of the inner surface of the shell wall. Walliser (1970) has described these markings, interpreting them as impressions of wrinkle-layer. On the internal mould of *Megaphyllites humilis* (Mojsisovics) the ritzstreifen form ridges and pits (Pl. 127, fig. 3). Near the umbilicus they are spirally arranged ridges; at mid-flank more or less radial pits and ridges; radially arranged pits, alone, form the outer part; and on the outer third all markings disappear. They are most prominent near the aperture. Behind the aperture they fade, and a quarter-volution back, those on the flank have disappeared. The spiral marks near the umbilicus persist further, to an unknown extent. Mojsisovics (1873, p. 47) mentions that *Megaphyllites humilis* shows wrinkle-layer as well as ritzstreifen but it is not shown on his illustrations, nor is it visible on the specimens I have examined. The markings have an appearance not unlike the impression of wrinkle-layer. However there is no evidence that they are impressions of a thin discrete layer encrusting the inner wall of the body chamber in the way that wrinkle-layer encrusts the test on the dorsum.

The ritzstreifen of *Nathorstites macconnelli* (Pl. 125, fig. 4), like those on the outer flank of *Megaphyllites humilis*, form pits in the internal mould. On the illustrated specimen they are most prominent on the inner third of the flank at the posterior part of the body chamber. Towards the venter and also in an adoral direction they fade and eventually disappear. Comparable, but less prominent, ritzstreifen are present on GSC No. 28231 (although not visible on Pl. 124, fig. 3). Most specimens of *Nathorstites macconnelli* show no ritzstreifen; whether this indicates that their presence is rare, or depends on the preservation, is not known.

Relationship between wrinkle-layer and Ritzstreifen. The evidence provided by Triassic ammonoids suggests that wrinkle-layer was deposited only on the dorsum and in the

EXPLANATION OF PLATE 127

Specimens coated with ammonium chloride. Arrows mark position of last septum.

Figs. 1 (×1), 2 (×16). *Drepanites hyatti rutherfordi* McLearn. Topotype, GSC No. 28021. Pardonet Formation, McLay Spur, Peace River, British Columbia (GSC loc. 9146). Middle Norian, Rutherfordi Zone. Partly internal mould, partly with outer test. Small patch of wrinkle-layer (fig. 2) present about one-quarter volution beyond aperture.

Fig. 3 (×4). *Megaphyllites humilis* (Mojsisovics). GSC No. 28022. Hallstatt Limestone, Sandling, Austria. Upper Carnian, *Tropites subbullatus* Zone. GSC loc. 19548 (Exchange from Stanford University, LSJU loc. 28187). Last half whorl is internal mould with impression of mouth border and ritzstreifen.

Figs. 4 (×1), 5 (×16). *Sageceras haidingeri* (Hauer). Geol. Bundesanstalt, Vienna, No. 2467. Hallstatt Limestone, Raschberg, Austria. Lower Carnian, *Trachyceras aonoides* Zone. Phragmocone with slightly abraded outer test. Fig. 5 shows surface at beginning of outer whorl and is part illustrated in Mojsisovics (1873, pl. 24, fig. 2).

Fig. 6 (×1). *Muensterites glaciensis* (McLearn). Topotype, GSC No. 9536. Talus, west slope East Glacier Spur, Peace River, British Columbia (GSC loc. 9797). Upper Ladinian, Sutherlandi Zone. Portion with smooth ribs is internal mould; with tuberculate ribs, outer test.